

V. *The Terminal Abdominal Structures of the Primitive Australian Termite, Mastotermes darwinensis Froggatt.*
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PLATE IV.

THROUGH the kindness of Dr. R. J. Tillyard I have been able to examine a few specimens of the extremely interesting Australian termite, *Mastotermes darwinensis* Froggatt, preserved in spirit. Since these insects are in some respects among the most primitive representatives of the order Isoptera, and since they are available for study to but few fortunate individuals, it may possibly be of some interest to describe briefly their terminal abdominal structures, which have not been figured before, so far as I am aware. The terminology here applied to the parts is that proposed for insects in general in a paper dealing with the terminal structures of male insects, published in the June 1918 issue of vol. xiii of the Bulletin of the Brooklyn Entomological Society (pp. 49-68), and in an article dealing with the terminal structures of female insects, published in the December 1917 issue of vol. xxv of the Journal of the New York Entomological Society (pp. 225-237).

There were two types of winged specimens in the material which I examined; but since I was permitted to retain only one winged specimen (which I wished to keep intact for a further study of the external morphology of these insects, and for a comparison with other termites) I have been unable definitely to determine, by dissecting them, which of the winged forms are males, and which are females. In the alate forms of many termites, however, the males bear styli and the females do not, and from what is known of related forms, I think that we are justified in assuming that in the winged caste of *Mastotermes* also, those forms which bear styli are males, and those which do not are females; but until this point has been definitely determined by dissection, the interpretation here given must be regarded as purely provisional. I might state, however, in this

connection, that I have dissected specimens of *Termopsis angusticollis* Hagen, which are placed in the family Protermitidae (to which *Mastotermes* also belongs) by Holmgren, and an examination of these forms has served to substantiate the conclusions here drawn concerning the sexes of the alate caste of *Mastotermes*.

In both types of winged forms of *Mastotermes* (Pl. IV, figs. 1 and 2), there are ten visible tergal plates in the abdomen. The sternal plates, however, are not situated immediately below their corresponding tergal plates in the posterior region of the abdomen, and the number of sternal plates is not the same in the two sexes, there being but six apparent, well-developed, pigmented, sternal plates in the winged forms which I have interpreted as the females, while there are eight of these sternal plates in the winged "males." In both forms the sternal plate of the real first abdominal segment has become atrophied (or at any rate, it cannot be readily detected), so that what appears to be the first abdominal sternite, is in reality the sternite of the actual second abdominal segment, while what appears to be the second sternite, is in reality the sternite of the actual third abdominal segment, and so on.

As was mentioned above, there are apparently but six distinct ventral plates in the abdomen of the winged "female" of *Mastotermes*, and since what appears to be the first sternite is in reality the sternite of the actual second abdominal segment, etc., the apparent sixth ventral plate ("hg" of Pl. IV, figs. 1 and 3), which is unusually large, represents the sternite of the actual seventh abdominal segment. This is in agreement with the statement made by Holmgren, 1909, on page 150 of his "Termitenstudien," that the seventh sternite is much larger than the others in the abdomen of female termites in general.

I at first thought that the stippled terminal area of the seventh abdominal sternite shown in Pl. IV, figs. 1 and 3, might represent the remains of another abdominal sternite entering into the composition of the unusually large sternite "hg," since in the alate females of our Californian Protermitid *Termopsis* (which are more primitive than those of *Mastotermes* in having retained a distinct sternite behind the seventh abdominal sternite) a distinct, though small, eighth sternite occurs in approximately the same position as that occupied by the terminal stippled area of the sternite labelled "hg" in Pl. IV, figs. 1 and 3. The condition

exhibited by the seventh abdominal sternite of the female soldiers and workers of *Mastotermes* (text-figure 1), however, would indicate that the stippled terminal area of the sternite labelled "hg" in Pl. IV, figs. 1 and 3 does not represent the remains of a formerly distinct sternite. The area in question was of greater extent in the alate female shown in fig. 1 than in the one depicted in fig. 3, and I

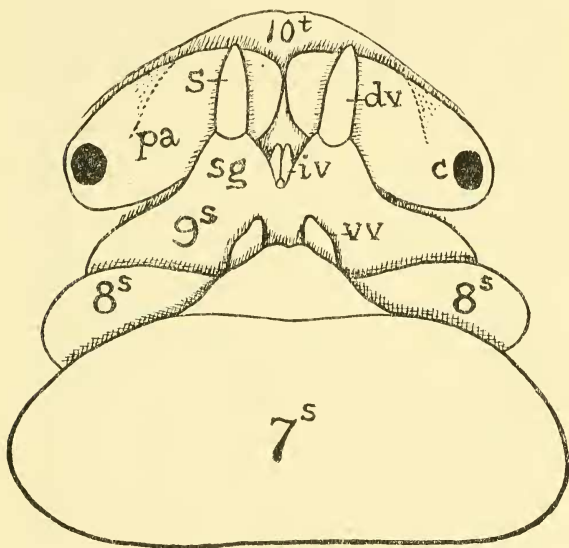


FIG. 1.—Terminal ventral abdominal plates of a female of the soldier caste of *Mastotermes*. For interpretation of lettering, see list of abbreviations at end of article.

am inclined to think that the latter is the more typical in this respect, although I have not been able to examine any other specimens of *Mastotermes* in order to determine this point.

Holmgren, 1911, on page 32 of the second part of his "Termitenstudien," quotes the following from a paper by Silvestri (which I have been unable to obtain) in describing the abdomen of the female of the worker caste of *Masto-*

termes: "Abdominis sternum septimum in parte postica mediana angustatum, productum, margine postico sinuato, sternum octavum et nonum nondum obtegens. Sternum octavum appendicibus genitalibus duabus brevibus; sternum nonum stilis instructum." Since the abdomen of females of the soldier caste is similar to that of the worker caste, the above-cited description applies equally well to the female soldier depicted in text-figure 1 of the present paper, since in the figure in question the seventh abdominal sternite is narrowed posteriorly in the median region, it is somewhat produced, its posterior margin is sinuate, and it projects slightly over the eighth and ninth sternites. The eighth sternite likewise bears two "genital appendages" (labelled "vv" in text-figure 1), and the ninth sternite bears a pair of styli "s." I find in addition, however, a third pair of appendages labelled "iv," which are very small, and on this account apparently escaped Silvestri's attention, although they occur in the females of both soldiers and workers. The intermediate appendages, labelled "iv" in text-figure 1, occur between the bases of the styli, labelled "sg." There is some indication that they may possibly belong to the sternite behind the ninth (*i. e.* the partially atrophied tenth sternite) which would be in agreement with the claim made by Dr. Wheeler, that the intermediate valves of the ovipositor belong to the tenth segment of the embryo (and come to have their position between the dorsal valvulae of the adult as a later modification), but my material was too poorly preserved definitely to determine this point.

Dr. Walker (Canadian Entomologist, vol. li, 1919, pp. 131-139), following Wood-Mason, Handlirsch, Berlese, and others, would interpret the dorsal valves of the ovipositor of Orthopteroid insects as representing the styli together with their basal portions "sg" (text-figure 1), from his studies on *Grylloblatta*; and the condition exhibited by the females of the worker and soldier castes of *Mastotermes* would uphold this view, for it is quite evident that the ventral appendages labelled "vv" in text-figure 1, represent the ventral valves of a primitive ovipositor, while the appendages labelled "iv" represent the intermediate valves, and the styli "s," with their basal portions "sg," apparently enter into the composition of the dorsal valves of the ovipositor of the Orthopteroid forms (see also figures of "*Blatta*," by Wood-Mason). The presence

of this primitive type of ovipositor in *Mastotermes* furnishes further evidence of the rather close relationship between *Grylloblatta* and the termites.

In the winged "males" of *Mastotermes* there are eight apparent abdominal sternites, as was mentioned above; but since the apparent first sternite is in reality the sternite of the actual second abdominal segment (the sternal plate of the first segment being atrophied, or so greatly reduced as to be no longer readily detected), the apparent eighth sternite, labelled "ha" in Pl. IV, figs. 2 and 4, represents the sternum of the actual ninth abdominal segment. In the males of *Grylloblatta campodeiformis* Walker, recently figured by Dr. Walker (*l. c.*), the hypandrium, or sternite of the ninth abdominal segment (situated below the genital apparatus of the male) bears a pair of distinct structures, the coxites, or styligers, to which the styli are attached. In the winged male of *Mastotermes* (fig. 4) the styligers "sg" (which may or may not represent the coxal segment of a limb, since the styli themselves are sometimes secondarily segmented) have become greatly reduced, and are partially united with the hypandrium "ha," but traces of them are still retained. A similar condition occurs in the cockroach *Cryptocercus*, shown in fig. 92 of the paper on the genitalia of male insects (Bulletin of the Brooklyn Ent. Soc., vol. xiii, 1918); but I did not realise the true significance of the styli-bearing structures in this insect (*i. e.* the homologues of the styligers "sg" of figs. 2, 4, etc.) until Dr. Walker had published his figures of the condition occurring in the primitive insect *Grylloblatta*.

In connection with the discussion of the styli, "s," and the styligers, "sg," I would call attention to the fact that if one compares Dr. Walker's figure 2 (Can. Ent. vol. li, plate viii) of the ventral region of the terminal abdominal segments of a male *Grylloblatta* with my figure 34 (Bull. Brooklyn Ent. Soc., vol. xiii, plate 4) of the same region of a male *Embia*, the resemblance between the two is very striking. The outline and relative size of the ninth sternite are very similar in both insects, and the so-called two-jointed cerci of *Embia* are remarkably similar to the two-jointed styli (*i. e.* the styli with their basal structures the coxites or styligers) of *Grylloblatta*, not only in position, but in the number and character of their component parts. Dr. Walker, however, maintains that these two structures are not homologous in the insects in question,

and provisionally, at least, I have accepted his verdict in the matter.

The cerci, labelled "c" in all figures, are fairly well developed in *Mastotermes*; but the segments of the cerci are not as distinct as in *Termopsis* (which is another feature in which *Termopsis* is more primitive than *Mastotermes*). There are traces of at least five segments in the cerci of *Mastotermes*, and in all probability several more have fused to form certain of the larger segments.

The paraprocts, "pa," or lateral plates of the eleventh segment, which bear the cerci, are quite well developed in *Mastotermes*, as is also the case with the tenth tergite "10t." The posterior margin of the tenth tergite of the winged male (fig. 2, "10t") is "indented" (or slightly emarginate) mesally, while the posterior margin of the tenth tergite of the winged female (fig. 1, "10t") is entire, and is somewhat "thinner," being more decurved posteriorly than is the case in the winged male.

In previous papers, I have applied the term "epiproct" to the tenth or to the eleventh abdominal tergites indiscriminately, and I have also employed this term as practically synonymous with the designation "pygidium." In the interest of exact usage, however, I would now suggest that the term "epiproct" be restricted to the eleventh abdominal tergite (which is distinguishable in but few insects), while some form of the designation "pygidium" should be employed for the apparent terminal tergite in other cases.

The term "pygidium" is frequently applied to the apparent terminal tergite in higher insects, regardless of whether one is dealing with the actual sixth, seventh, eighth, ninth, or tenth tergite, the actual terminal tergites in such cases being usually withdrawn or "telescoped" beneath the apparent terminal tergite which conceals them, so that what appears to be the terminal tergite or "pygidium," is not actually the terminal one under these conditions. It would be much more exact when this is the case, to prefix to the term pygidium, the Greek designations hexa-, hepta-, octo-, ennea-, or deca-, to indicate that the apparent last tergite is actually formed by the tergite of the sixth, seventh, eighth, ninth, or tenth segment, as the case may be. Thus, the so-called "pygidium" of certain Coleoptera is in reality formed by the tergite of the sixth abdominal segment (the terminal ones being usually with-

drawn beneath it), while the so-called "pygidium" of a cockroach or termite is usually formed by the tergite of the tenth abdominal segment; and in the interest of exact usage, it would be preferable to distinguish between these two types of "pygidia" by designating that of the beetle a "hexapygidium" and that of the cockroach or termite a "decapygidium."

The condition occurring in the terminal abdominal structures of the winged "male" of *Mastotermes* lends additional weight to the view that the termites are rather closely related to the cockroaches, since in both groups the pygidium, "10t," is a "decapygidium" (*i. e.* it is formed by the tenth tergite), the paraprocts "pa" are usually well developed in both types of insects, and in the male of the primitive cockroach *Cryptocercus*, referred to above, there are traces of the styli-bearing structures "sg" which are only partially united with the ninth sternite "ha" as in *Mastotermes* (fig. 4). On the other hand, the genitalia of *Mastotermes* and other termites do not exhibit the well-developed, asymmetrical penis valves characteristic of most cockroaches, Mantids, and Zoraptera; and since the termites belong to the superorder Panisoptera (composed of the Isoptera, Zoraptera, Mantodea, Blattodea, etc.), it is rather surprising that such primitive forms as *Mastotermes* should not exhibit some indications of such a widespread condition occurring in the bulk of their relatives in this group. It is possible, however, that since some termites such as those here discussed have been found to have developed a primitive type of ovipositor (a condition occurring extremely rarely among Isoptera), still others will be found in which traces of the penis valves are retained. Indeed, in the winged males of *Termopsis*, there are traces of the penis valves, but they are so small and delicate that one can scarcely see them, and they are quite unsatisfactory for a comparative study of the structures in question.

In Vol. 21, 1919, of the Proceedings of the Entomological Society of Washington (pp. 129-151), in an article dealing with the terminal abdominal structures of the most primitive representatives of the Hymenoptera (*i. e.* the sawflies), it was shown that the hypandrium, or plate below the male genitalia ("ha" of Pl. IV, figs. 2 and 4), is in most insects formed by the sternite of the ninth abdominal segment, or those preceding it, rather than by the tenth sternite, as was formerly claimed. Furthermore, as is the case in

Mastotermes, the sternite of the seventh, or preceding segments, as well as the eighth sternite, may form the plate below the genital apparatus of female insects in general.

In comparing together the terminal structures of insects in general, I have been impressed with the marked resemblance between the terminal structures of the sawflies and those of the termites (with the exception of the genital apparatus of the males, since the styli of male termites apparently become modified to form clasping organs in the male sawflies), and there are a number of features which point to a rather close relationship between the two groups. These resemblances have led me to conclude that the Psocidae (*s. l.*), Hymenoptera, Mecoptera, Neuroptera, and Coleoptera probably arose from ancestors anatomically intermediate between the Isoptera (with the Zoraptera) on the one hand, and the Dermapteron-Embiid-Plecopteron group on the other. Furthermore, the Isoptera are themselves intermediate between the Blattodea (with the Mantodea) and the Dermapteron-Embiid-Plecopteron group, and because of this phylogenetically important position which they occupy with relation to the lines of descent of the other orders of insects, their anatomy should be more carefully studied than has been the case heretofore.

I have suggested in previous papers, that the Palaeodictyoptera, Ephemera and Odonata might possibly be associated together in a section of the Pterygotan insects, and while this arrangement holds good for certain of the Palaeodictyoptera, it is not true of all the insects included in this order, which appears to be a very heterogeneous conglomeration of insects, of which certain forms are not sufficiently nearly related to be included in the same order, or even superorder. Thus for example, I would now consider such Palaeodictyoptera as the Stenodictyoids (or those related to *Stenodictya*) as belonging in the superorder Panplecoptera, which includes the Plecoptera, Embiidea, Dermaptera, Coleoptera and their allies (to which might be added such fossil forms as the Hadentomodea, Haplopterodea, etc., although I am not certain as to such forms as the Sypharopterodea). On the other hand, some of the insects now placed in the order Palaeodictyoptera, such as the Eubleptidae, bear a strong resemblance to the insects comprising the superorder Panplectoptera, composed of the Ephemera (also called Plectoptera), Protephemerida (*Triplisoba*) and their allies. Handlirsch would derive

